

Scale-dependent portfolio effects explain growth inflation and volatility reduction in landscape demography

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Edited by Alan Hastings, University of California, Davis, CA, and approved October 10, 2017 (received for review March 13, 2017)

Population demography is central to fundamental ecology and for predicting range shifts, decline of threatened species, and spread of invasive organisms. There is a mismatch between most demographic work, carried out on few populations and at local scales, and the need to predict dynamics at landscape and regional scales. Inspired by concepts from landscape ecology and Markowitz's portfolio theory, we develop a landscape portfolio platform to quantify and predict the behavior of multiple populations, scaling up the expectation and variance of the dynamics of an ensemble of populations. We illustrate this framework using a 35-y time series on gypsy moth populations. We demonstrate the demography accumulation curve in which the collective growth of the ensemble depends on the number of local populations included, highlighting a minimum but adequate number of populations for both regional-scale persistence and cross-scale inference. The attainable set of landscape portfolios further suggests tools for regional population management for both threatened and invasive species.

population demography | scale dependence | growth inflation | volatility reduction | demography accumulation curve

Population demography describes composite features of scaling up from individuals, each with different risks, to populations. It has been studied since Malthus (1). However, it is not straightforward to predict the dynamics of regional ensembles of populations from single populations; scaling up may require a different set of conceptual tools (2). Although most demographic studies of natural populations of plants and animals are conducted at local scales and on few (three or fewer) populations (3), we are often concerned about the behavior of ensembles of populations. When appropriately scaled-up to population ensembles, demography is potentially valuable for understanding many fundamental and applied problems, including risk of regional extinction, biological invasions, pathogen spread, fisheries management, and as the foundation for natural selection. To this end, the concept of landscape demography has been introduced to emphasize the collective behavior of population ensembles across spatial scales (4).

Landscape demography is a generalization of the special case of metapopulation theory and conceptually brings together several approaches and theoretical lines of work. In classic metapopulation theory (5, 6), population persistence at the regional or landscape scale is ensured through the dynamic colonization-extinction balance from recolonization of suitable sites. In scale transition theory (7, 8), with the full knowledge of recruitment and dispersal of all populations over an infinite landscape, the landscape-level multiplicative growth rate can be partitioned into the average growth rate of local populations plus the growth-density covariance (see also ref. 9). The landscape-level persistence can thus be elevated by having positive growth-density covariance. Under similar premises, landscape-level growth rate can be further inflated by affecting the growth-

density covariance from temporal fluctuation and autocorrelation in local population growth rate driven by environmental noise (9–11). Such red noise could further drive intermittent rarity of population dynamics (12) and facilitate invasive establishment (13). Moreover, through connecting local stochastic processes via redistributing individuals, system-level persistence and growth can be achieved (14, 15) through stochastic resonance (16–18). By highlighting the roles of positive growth-density covariance, temporal variability and red noise, redistribution, and spatial heterogeneity these stochastic metapopulation and demographic theories have laid the foundation for connecting local- to landscape-level demography.

Our goal here is to extend this theory by scaling up demography by continuously adding local populations into the landscape ensemble, even when dispersal and the nonlinear population growth function are not explicitly quantified and when some populations are ignored due to limited sampling effort. Economic portfolio theory provides such a framework that can be extended for analyzing the dynamics of ensembles of populations. With this approach dispersal may be incorporated, but the ensemble can be a set of populations without colonization between them, rather than a set of connected subpopulations (as in metapopulation ecology). In this framework, we start with three quantities that are essential for analyzing the

Significance

Population demography is central to many problems in ecology, evolution, and conservation biology, yet there is a gap between the information needed about the demography of population over multiple spatial scales and the available data, which are largely local. Inspired by concepts from landscape ecology and Markowitz's investment portfolio theory, we address this lacuna by developing a method for quantifying and predicting the demography of multiple populations across spatial scales and apply it to gypsy moth populations. We show that population demography is scale-dependent due largely to a tilted portfolio effect from skewed population size distributions and covarying population growth rate; this explains why population ensembles can have growth rates greater than the mean with variance smaller than the mean.

Author contributions: C.H., G.A.F., and J.G. designed research; C.H., G.A.F., and J.G. performed research; C.H. and G.A.F. contributed new reagents/analytic tools; C.H. and G.A.F. analyzed data; and C.H., G.A.F., and J.G. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1704213114/-DCSupplemental.

stochastic demography of population ensembles (19): means, variances, and covariances of local population change rates. Note that the choice of specific metrics of population change rates assume the normality or at least symmetry of measured rate distributions around the mean (discussed below). The first two are indicators of population viability that can be driven by many environmental and ecological factors, such as habitat quality, disturbance, and biotic interactions including density dependence, interspecific competition, and predation. These two quantities have also been highlighted in other demographic theories. The covariance measures synchrony between populations (20) and reflects a range of drivers, including the Moran effect of broad-scale environmental forcing (21–23), cross-trophic or intraspecific biotic interactions (24, 25), distance decay of similarity (26–28), and cross-population migration (29–31). The role of the covariance between local population change rates has not been fully explored in previous demographic theories. Those specific aspects of population demography that have been highlighted in previous theories, such as the growth-density covariance and temporal autocorrelation, are considered later in an expanded formulation of our approach. To transform our understanding of how local demography contributes to the collective behavior of regional ensembles, landscape demography also needs to formulate how these quantities depend on the number of local populations in the ensemble, so that drivers of the demography of the ensemble can be sought and inferences made across relevant scales.

Fortunately, we can borrow from economic theory to address this problem. Models to predict rates of change and minimize volatility for portfolios of assets are well established in economic theory, employing portfolio diversification and constrained optimization to identify financial strategies for ensembles of individual investments (32, 33). The dynamics of both biological populations and investment portfolios typically are characterized by substantial fluctuations of individual units (populations and assets) but smaller fluctuations for ensembles of those units (34, 35). We approach scaling from single populations to an ensemble by borrowing methods for portfolio diversification across populations from these investment models (32, 33). Modern portfolio theory is based on the return, $R = (n_{t+1} - n_t)/n_t$, with n_t the investment size at time t . However, the return for biological population size n is often highly nonnormal, as is the multiplicative growth rate, $\lambda = n_{t+1}/n_t$ (10), making the mean and variance invalid metrics for the centroid and spread of return (see the gypsy moth example below). Instead, the relative growth rate (RGR), $r = \ln(n_{t+1}/n_t)$ is approximately normal. In what follows, we only address the case for positive population size ($n_t > 0$). In the event of a local extinction followed by recolonization, the newly established population is considered to be a new local population in the ensemble.

We propose a platform of landscape demography inspired by modern portfolio theory but using RGR rather than return R or multiplicative growth rate λ . This permits the study of the demography of an ensemble of populations while accounting for the potential interconnections between populations that reflect multiple demographic and environmental factors including not only dispersal but also shared environmental and biotic forcing. We first advance models for this platform, emphasizing the connections that allow scaling up from local dynamics to the collective behavior of many populations at landscape and regional scales. We then demonstrate this platform by scaling up the demography of gypsy moths (*Lymantria dispar*) in the northeastern United States by pooling populations into larger ensembles.

Analytical Results

Let there be z populations in the landscape. The landscape portfolio is the weight vector of populations: $\vec{w} = \{w_1, w_2, \dots, w_z\}$ subject to $w_i \geq 0$ and $\sum_i w_i = 1$, with $w_i = n_i/n_U$, where n_U is the

sum of population sizes. Generally, n_i follows a lognormal distribution (10) and thus the RGR, r_i , a Gaussian, with expectation μ_i , variance σ_i^2 , and $\sigma_{ij} = \text{cov}(r_i, r_j)$. The ensemble RGR is

$$r_U = \ln \left(\sum_i e^{r_i} w_i \right). \quad [1]$$

Following ref. 15, we first present the formulae of landscape demographies for constant weights (called the rebalancing strategy in economic theory) and then extend the formulae later to connect with other stochastic demography theories. Nonetheless, the possible demographies of landscape ensembles are addressed here by exploring the entire feasible range of weights. To find the expectation (μ_U) and variance (σ_U^2) of the ensemble (U) RGR, let $\nabla = \sum_i e^{\mu_i + \sigma_i^2/2} w_i$ and $\Delta^2 = \sum_i \sum_j e^{\mu_i + \sigma_i^2/2} e^{\mu_j + \sigma_j^2/2} (e^{\sigma_{ij}} - 1) w_i w_j$; we then have

$$\begin{aligned} \mu_U &= \ln \left(\nabla^2 / (\nabla^2 + \Delta^2)^{1/2} \right) \\ \sigma_U^2 &= \ln \left((\nabla^2 + \Delta^2) / \nabla^2 \right). \end{aligned} \quad [2]$$

Two landscape ensembles are also synchronized to some extent due to covarying populations (Eqs. S4 and S12).

The attainable set is the set of all possible landscape portfolios. It is useful to describe the attainable set by its projection in the growth-volatility (μ_U, σ_U^2) plane; its boundaries (Fig. 1A) describe demographies for combinations of two or more populations, with single-population portfolios at the ends of each two-population curve. The top-left boundary (Fig. 1A) is of

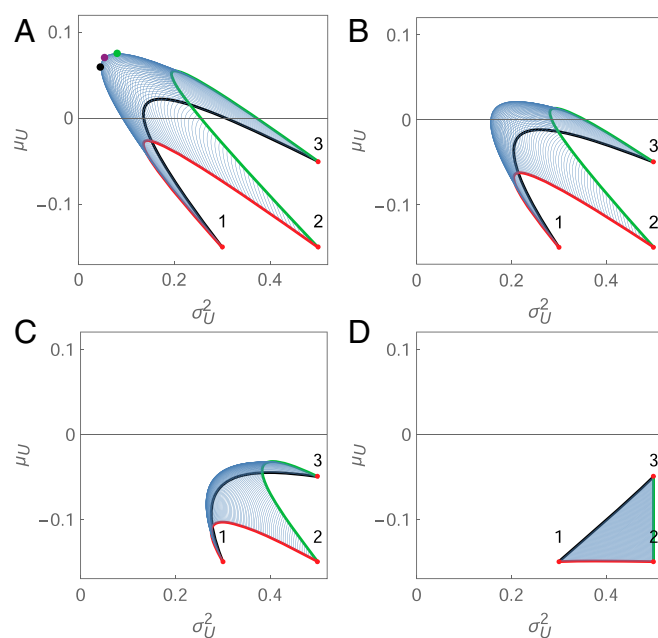


Fig. 1. Expectation and variance of RGR for an ensemble of three populations. Red, green, and black curves: attainable sets for combinations of two populations ($w_i + w_j = 1$). Blue mesh: attainable sets for combinations of three populations ($w_1 + w_2 + w_3 = 1$). Covariances between populations are the same in each plot and are calculated as the correlation (ρ) times the SDs of the two populations ($\sigma_{ij} = \rho \sigma_i \sigma_j$). (A) $\rho = -0.5$; (B) $\rho = 0$ (independent); (C) $\rho = 0.5$; (D) $\rho = 1$ (perfectly synchronized). The efficient frontier is calculated by minimizing $x(\sigma_U^2/2) - (1-x)\mu_U$ for specific x values; $x = 0$ for the maximum growth portfolio (green dot in A), $x = 1$ for the minimum variance portfolio (black dot in A), and $x = 1/2$ for the portfolio on the efficient frontier where the attainable set is stretched the most along the ensemble shifting direction (purple dot in A).

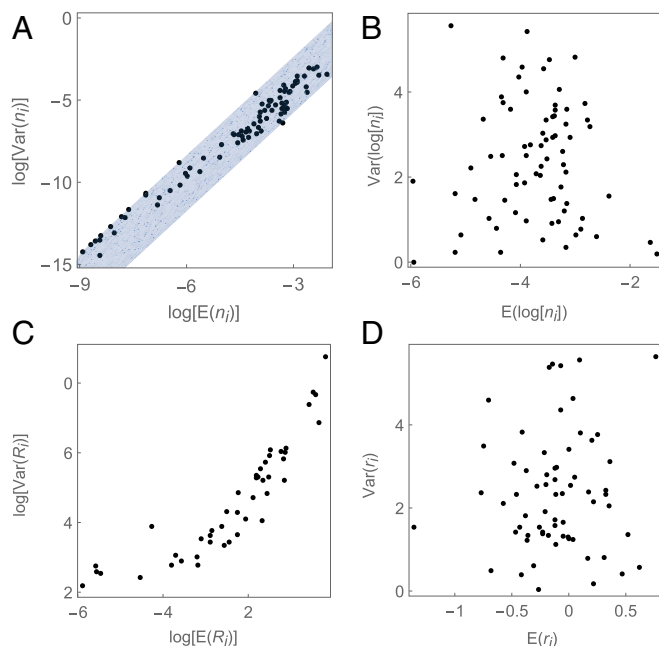


Fig. 3. Features of the population size and demography of the gypsy moth in the northeast United States. (A) The log-transformed relationship between the temporal expectation and variance of population size, with each point representing a local population, all located within a thin belt around a power law. (B) The relationship between the temporal expectation and variance of log population size, showing the power law in A to be artificial due to the skewed distribution of population size. (C) The log-transformed relationship between expectation and variance of the return, showing the distribution within a narrow belt. (D) The relationship between the expectation and variance of the RGR, justifying its use as an unbiased metric of population demography.

population demography for *L. dispar* is provided in Fig. 3, with the notable statistical artifact of Taylor's power law from a skewed size distribution (42). We were able to calculate means and (co)variances of local population RGRs (Dataset S1) for 38 quadrats (Figs. S4 and S5). The DAC of μ_U demonstrated a clear upward trend with an increasing number of included populations, shifting from negative to positive at $z = 30$ (Fig. 4A), indicating growth inflation. The DAC of σ_U^2 eventually declined when $z > 15$ (Fig. 4B), indicating volatility reduction through portfolio diversification. The annual ensemble RGRs (blue lines in Fig. 4C) fluctuated strongly within a belt perpendicular to the efficient frontier, showing that the annual ensemble RGR and its variance are negatively correlated (as expected in a system prone to massive outbreaks). The DACs of gypsy moths point to a minimum of 30 local populations to be monitored for meaningful, qualitatively correct, regional inference.

Conclusions

The theory developed here provides tools for estimating ensemble mean RGRs and their variances, which may change nonlinearly across scales (i.e., the DAC). Useful extensions of this theory may include the role of nonstationarity, density dependence, and spatial autocorrelation in time series. The gypsy moth example suggests a strategic approach for invasive species: If we can drive ensembles below the sizes at which growth inflation and/or volatility reduction operate, we may be able to achieve regional control; for threatened species, there can be a critical threshold for the number of populations below which regional extinction is likely. These results point to mechanisms of regional persistence that do not follow from local demographic results and are not possible under classic metapopulation models,

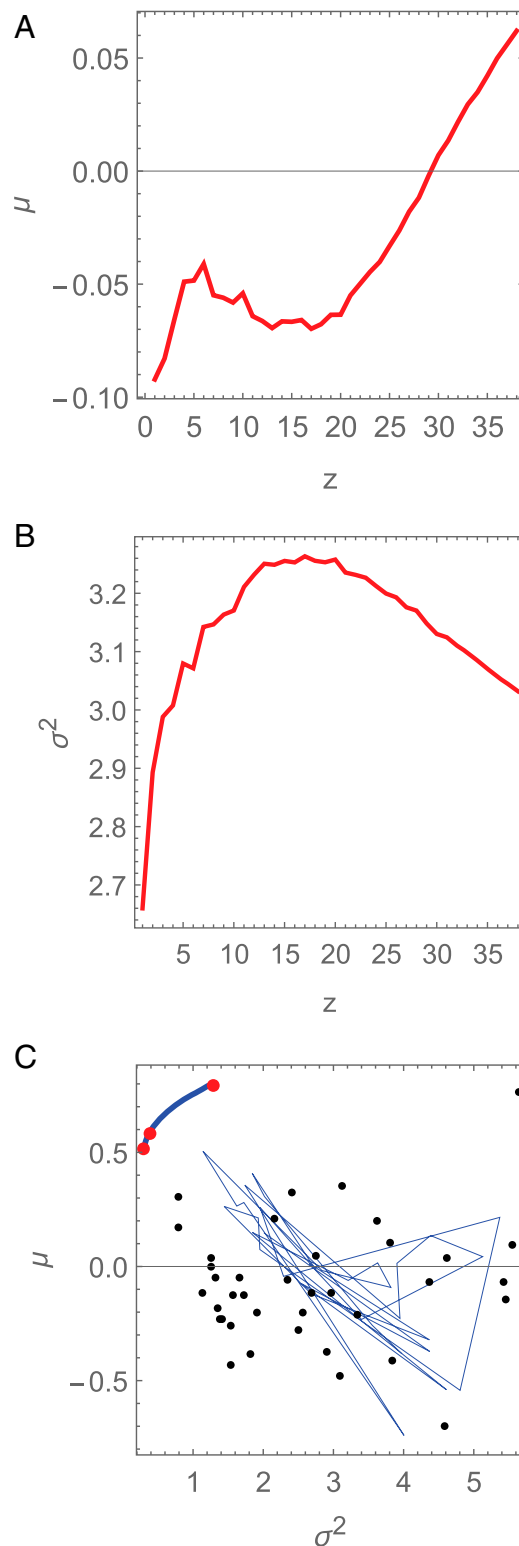


Fig. 4. Landscape demography and DACs of 38 gypsy moth populations. Accumulation curves for expectation (A) and variance (B) of ensemble RGRs as a function of the number of included local populations (z). Red lines: averages of 1,000 rarefaction curves. (C) Black dots: expectation and variance of the RGR for specific populations (Fig. 3 and Dataset S1). Blue lines: demographic trajectory for the ensemble. Blue curve: efficient frontier for the ensemble, calculated as in Fig. 1 (Dataset S2).

where regional persistence results from a dynamic colonization–extinction balance. Persistence in a landscape portfolio can be enhanced through inflated growth and reduced volatility largely due to the tilted portfolio effect for covarying populations with comparable magnitudes of variability, which is distinct from existing stochastic demography theories that focus on the roles of growth–density covariance, temporal autocorrelation, and stochastic resonance. Finally, the attainable set of landscape portfolios and the DAC of ensemble mean and variance suggest tools for regional population management for both threatened and invasive species through changing the relative weights and other demographic quantities of, as well as the covariance between, target populations and pinpointing the minimum number of populations for reliable regional-scale decision making.

Materials and Methods

We used population time series to calculate annual RGRs of local populations and their means, variances, and covariances; expected ensemble

RGR and its variance are found from these using properties of the log-normal distribution. Plotting the expected ensemble RGR and its variance, for all possible relative weights of local populations, permits visualization of the possible ensemble growth rate and its variance and identification of the maximum RGR given a level of volatility. We derive a general expression for the expected ensemble RGR, permitting connections to other theories of stochastic demography. We introduce the DAC, the expectation and variance of ensemble RGR as a function of the number of local populations. The DAC, as estimated with rarefaction curves from gypsy moth populations, permits inference on the action of growth inflation and volatility reduction.

ACKNOWLEDGMENTS. We thank A. M. Liebhold for *Lymantria* data, R. D. Holt for discussion, and the editor and two anonymous reviewers for constructive comments. This work is supported by the Stellenbosch Institute for Advanced Studies as fellowships (to G.A.F. and J.G.); the South African Research Chair Initiative, National Research Foundation of South Africa Grants 89967 and 109244, and Australian Research Council Grant DP150103017 (all to C.H.); and National Science Foundation Grants DEB-1120330 and DEB-119891 (to G.A.F. and J.G.).

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